

of the Golgi apparatus (Dalton & Felix, 1954; Dalton & Felix, 1955; Dalton & Felix, 1956). As illustrated in Figure 6.14, they differentiated three components – a system of lamellae or flattened cisternal sacs, large vacuoles, and clusters of small vesicles. The flattened sacs (saccules) typically occur in stacks of three to seven in plant and animal tissues, and in larger numbers in unicellular organisms. The saccules are the major contributor to the traditional image of the Golgi apparatus in light microscopy. On one side, the *cis* side, the stacks abut the endoplasmic reticulum. Clusters of small vesicles are visible at the interface between the endoplasmic reticulum and the *cis* side of the stack. On the other side, the *trans* side, of the stack, larger vacuoles are found that are often referred to as condensing vacuoles. To highlight the fact that there are several different components comprising the Golgi region, Dalton introduced the term *Golgi complex*. In addition to providing much better images of the Golgi apparatus than had been available through light microscopy, Dalton and Felix also sought to address its functional significance. By comparing the images of the Golgi complex in mouse intestinal cells after fasting and forty minutes after eating, Dalton and Felix provided evidence that the Golgi apparatus is involved in storage of lipids after absorption.

Other early electron micrographs of the Golgi apparatus (Sjöstrand & Hanzon, 1954; Farquhar & Rinehart, 1954) revealed a close relation between secretory granules and the Golgi apparatus. Subsequent micrographs seemed to show secretory granules within the Golgi structures:

Secretory granules have been seen within components of the Golgi bodies of rat pituitary acidophils and mouse pancreatic acinar cells. The fact that secretory granules are much more frequently encountered within Golgi components under conditions of increased secretory activity suggests that granule formation may occur within the Golgi apparatus in these two types of cells. (Farquhar & Wellings, 1957, p. 321)

Applying biochemical analysis required separating the Golgi apparatus from other cell components through cell fractionation. In addition to his electron microscopy of the Golgi apparatus, Dalton (Dalton & Felix, 1954) established that the Golgi apparatus could be extracted from epididymis cells, and Schneider and Kuff (1954) separated it within epididymal homogenates by gradient centrifugation. Schneider and Kuff produced evidence that the Golgi fraction was comprised of high concentrations of phospholipid as well as acid and alkaline phosphatase and RNA. However, fractionation of the Golgi apparatus was more challenging than fractionation of other organelles. Its smooth lipoprotein membranes, for instance, tended to break up and form smooth microsomes (Whaley, 1975, p. 31). A decade later Morré and his